

Shifting phenology and abundance under experimental warming alters trophic relationships and plant reproductive capacity

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Abstract. Phenological mismatches due to climate change may have important ecological consequences. In a three-year study, phenological shifts due to experimental warming markedly altered trophic relationships between plants and insect herbivores, causing a dramatic decline of reproductive capacity for one of the plant species. In a Tibetan meadow, the gentian (*Gentiana formosa*) typically flowers after the peak larva density of a noctuid moth (*Melanchra pisi*) that primarily feeds on a dominant forb (anemone, *Anemone trullifolia* var. *linearis*). However, artificial warming of $\sim 1.5^{\circ}\text{C}$ advanced gentian flower phenology and anemone vegetative phenology by a week, but delayed moth larvae emergence by two weeks. The warming increased larval density 10-fold, but decreased anemone density by 30%. The phenological and density shifts under warmed conditions resulted in the insect larvae feeding substantially on the gentian flowers and ovules; there was ~ 100 -fold more damage in warmed than in unwarmed chambers. This radically increased trophic connection reduced gentian plant reproduction and likely contributed to its reduced abundance in the warmed chambers.

Key words: alpine meadow; *Anemone trullifolia* var. *linearis*; biodiversity; *Gentiana formosa*; global warming; *Melanchra pisi*; phenological shift; trophic interaction.

INTRODUCTION

Species loss due to global warming has been attributed to increased abiotic stresses due to changes in temperature and rainfall (e.g., Helmuth et al. 2002, Schwartz et al. 2006) and/or to altered biotic species interactions, such as competitive exclusion (studied mostly among plant species; Klein et al. 2004, 2008, Gedan and Bertness 2009) and disruptions of trophic relationships (Schwartz et al. 2006, Memmott et al. 2007, Tylianakis et al. 2008). The trophic decoupling may be mostly due to phenological mismatches between abundances of plants and animals (Visser and Holleman 2001, Visser et al. 2004, Memmott et al. 2007, Bertin 2008, Tylianakis et al. 2008), which can lead to unexpected consequences in community species composition and ecosystem properties.

However, it is also possible for species under global warming to establish novel trophic connections or greatly expand weak connections. The historical record and experimental warming confirm that many plants advance their budding, leafing, and flowering timing with increased temperature (Visser and Holleman 2001, Visser et al. 2004, Memmott et al. 2007, Bertin 2008), but some species delay their emergence timing (e.g.,

Sherry et al. 2007). Similarly, animals (such as insects and migratory birds and mammals) often advance their emergence or migration timing (ostensibly) to match plant phenologies, but they are not always as plastic in this sense as plants, and sometimes animals may also delay their emergence timing (Visser and Holleman 2001, Visser et al. 2004). Such a wide range of responses makes it possible for temporal connections to be established or strengthened for species that typically are phenologically disconnected, and vice versa.

Furthermore, the abundances of both animals and plants may be changed by global warming. Many studies have suggested that outbreaks of insects and pathogens are more likely to occur under global warming (e.g., Myers and Knoll 2001, Taylor et al. 2007); plant species may also markedly change their abundances due to the effect of temperature increase on survival, growth, and competitive ability (e.g., Klein et al. 2004, 2008). Additionally, animals are often flexible in foraging and reproductive behaviors (e.g., Bale et al. 2002, Barton and Schmitz 2009) and thus able to adjust to climate alterations with rapid shifts in population density (Harrington et al. 2001, Bale et al. 2002). For example, invasive pest animals may exhibit population outbreaks when they are unintentionally dispersed into new habitats, by exploiting new food resources (e.g., Green-slade 2008). Thus, a dramatically enhanced or novel trophic relationship could be triggered if normal food plant resources are scarce, if consumer species are unusually abundant, and/or if potential novel food

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species are available and of suitable quality under warmed conditions, in agreement with optimal diet theory (Emlen 1966). Nevertheless, trophic relationships of this kind, and associated ecological consequences, have not been empirically documented in relation to warming.

In this paper, we report the result of a three-year experimental warming in a Tibetan alpine meadow, one of the most sensitive areas to global warming in the world (Klein et al. 2004, 2008). We demonstrated that a dramatic decline of reproductive capacity in the gentian (*Gentiana formosa*) was an outcome of a greatly expanded trophic connection between the plant and larvae of a moth species. Our study system consists of the moth species (*Melanchra pisi*, Lepidoptera: Noctuidae) and two of its host species, a historically typical food species (*Anemone trullifolia* var. *linearis*) and the rare food species (*Gentiana formosa*; Appendix A). Experimental warming changed the phenologies and abundances for the plant and insect species, and increasing the trophic relationship between the moth and the gentian, in which the moth larvae fed extensively on flowers and other reproductive structures.

METHODS AND MATERIALS

Study background and natural history

The experiment was located in an alpine meadow of Hongyuan County, Sichuan Province of eastern Qinghai-Tibetan Plateau, China (32°48' N, 102°33' E). The altitude is ~3500 m. The climate is characterized by short spring and autumn, a long winter, and a mild cool summer. The annual mean temperature is 0.9°C, with the mean maximum and minimum being 10.9°C and -10.3°C in July and January, respectively. Annual mean precipitation is approximately 690 mm, fluctuating greatly among years, 80% of which occurs during May to August. The annual mean period of snow cover is 76 days.

Vegetative cover of the meadow was over 90%, and average maximum plant height was ~30 cm. Vegetation was dominated by sedges such as *Kobresia setchwanensis* and *Kobresia pygmaea* and grasses such as *Deschampsia caespitosa* and *Agrostis matsumurae*. Forb species, including *Anemone trullifolia* var. *linearis*, *Potentilla anserina*, *Saussurea nigrescens*, *Gentiana formosa*, and *Thalictrum alpinum* were also abundant. The anemone was about 20 cm in mature height. Under current climate conditions it turns green and then flowers in early May; the aboveground vegetative growth does not senesce until late September. *Gentiana formosa* was less abundant than anemone, but was conspicuous because of its distinct blue flowers late in the growing season when there were no other flowering species. This gentian turns green in mid April and its aboveground parts senesce shortly after snowfall in October.

The pasture has been under intensive grazing for decades. Yaks (*Bos grunniens*) are one of the most

important livestock species reared by local people. Although rodent (Plateau zokors, *Myospalax fontanierii*) damage occurred in many areas surrounding our study site, there was no rodent activity observed until our study progressed to the third year (2009), when we detected damage to silverweed (*P. anserina*). In contrast, invertebrates were abundant in this pasture. Because yak dung density was high, the decomposer communities were diverse (Wu and Sun 2010). There was a very low density (<0.01 individuals/m²) of *Locusta migratoria manilensis* (Meyen) found in the mid growing season from late June to early August in some dry sites. However, this locust was absent in our study site possibly because of high soil moisture. In the late growing season from mid-August to mid-September, larvae of *Melanchra pisi* (Lepidoptera: Noctuidae (Hadeninae)) were active in wet sites. We did not observe apparent enemy species (such as birds and arthropods) preying on the larvae. This moth species was relatively abundant and may generally have stronger direct impacts than other aboveground insect species on plants in the study site.

The moth adults are nocturnal, but have also been observed during daylight hours. There is a single annual brood. Larvae emerge late in the growing season (August to October) and then pupate over winter; adults emerge the next summer. In the study site, we (Y. Liu, G. Li, S. Sun) observed that the moth larvae almost exclusively fed on anemone leaves, but also fed on reproductive structures of the gentian in warmed chambers in the first study year (2007). Thus, we focused on the population dynamics and phenologies for these three species.

Physical setting of the warming experiment

In June of 2007, 20 2 × 2 × 2 m open-top chambers (OTCs) were randomly deployed (at a minimum spacing of 3 m) in a fenced, flat area of about 0.5 ha. The sides of 10 OTCs were covered with thin (less than 0.1 mm) steel screen with a mesh size of 0.2 × 0.2 mm. The other half of the OTCs was covered with polycarbonate sheet, which was clear and smooth allowing a relatively larger warming effect than the steel screen. In mid-July of 2008, the transparency of the steel screen was 84.4% on average ($N = 5$ chambers) under full light conditions, slightly and insignificantly lower than that of the polycarbonate sheet (86.2%, $N = 5$ chambers; $t = 0.974$, $P = 0.358$). We refer to these two types of OTCs as the ambient, unwarmed, control chambers and the warmed chambers, respectively. Each OTC was sunk 10 cm into the soil and firmly stabilized to withstand extreme windy conditions anticipated at the site. Yak grazing was high before fencing but was precluded thereafter.

Two years of continuous measurements (thermometers at centers of the OTCs; DS1921G; Maxim Integrated Products, Sunnyvale, California, USA) showed that mean annual temperature at soil surface

and at 30 cm above ground surface was 1.3–1.6°C higher in the warmed than unwarmed chambers (Appendix B). Soil moisture was recorded once every two months during the experiment except for the freezing period (from November to March). There was no systematic and significant difference in soil moisture between warmed and ambient chambers (Appendix C: Fig. C1a). In contrast, a short-term record on atmospheric vapor pressure deficit showed that the air at 30 cm above the ground was often slightly drier in the warmed than in the ambient chambers (Appendix C: Fig. C1b).

Population survey and phenological observations

Within each OTC, one central 1.5×1.5 m subplot was used for plant and soil measurements and sampling, but the central part of that square (a 1×1 m area surrounded by a steel frame) remained intact and without any destructive sampling during the experiment. A 1-m^2 quadrat frame divided into 10×10 cm grids was used to facilitate the cover and density estimates. Species composition and plant cover were recorded for each chamber. No significant difference in cover was found for the anemone and gentian species between warmed and unwarmed chambers ($N = 20$ chambers, $t = 1.259$, $P = 0.224$) immediately after the OTCs were installed. At the end of the growing seasons of 2008 and 2009, we recorded plant height, density, and cover for both the anemone and gentian species for the central 1-m^2 part of each chamber.

Leaf and flower phenologies were followed for both the anemone and the gentian species; timing of larva emergence and abundance were also assessed for the central 1 m^2 subplot in each OTC. Detailed records were kept in 2008 and 2009 following less exact phenological observations in 2007. These records started from 1 July each year because the larvae did not emerge until August. The survey was conducted about once a week in 2008 but more frequently (about once every four days) in 2009. We recorded the number of open flowers for the gentian, the percent cover for the anemone, and the larva number for the moth in each OTC. Meanwhile, we estimated the damage of anemone leaves and gentian flowers and fruits.

Two measures were used to characterize moth damage to gentian flowers. One is flower damage level, estimated as the percentage of damaged flowers within a chamber. Flowers losing more than 20% of the area of their petals or other parts were classified as damaged. The other measure is the ratio of fruits initiated to total flowers opened. Initiated fruits were easily identified because their expansion within senescent flowers is easily detected if fertilization has been successful.

RESULTS

Warming effect on phenologies

Experimental warming substantially delayed the timing of peak density of moth larvae (Fig. 1). In 2008, the mean peak fell on Julian day 255 in the

warmed chambers, 15 days later than in control chambers (Fig. 1a and b), whereas in 2009 the delay was 13 days (Fig. 1c and d). In contrast, plant phenology was generally advanced by warming. Peak flowering of gentian was 8 days earlier in the warmed OTCs than in control chambers in 2008 (Fig. 1a and b), and 6 days earlier in 2009 (Fig. 1c and d). Similarly, warming significantly advanced the timing of aboveground senescence in the anemone species, with a change ranging between 5 and 8 days in 2008 and 2009 (Fig. 1).

Warming effect on abundances

The peak density of moth larvae was increased by experimental warming; it was 5.1 (2008) and 4.3 larvae/ m^2 (2009) in the warmed chambers, significantly greater than in the ambient chambers (less than 1 larva/ m^2 in both 2008 and 2009; $t = 3.452$, $P = 0.01$ and $t = 3.915$, $P = 0.003$, Fig. 1). The difference in density was small between years for both treatments (Fig. 1). Peak flower density of the gentian also varied between years and treatments (Fig. 1). Experimental warming significantly decreased gentian flower density by 25–50% in both 2008 and 2009 ($t = 2.818$, $P = 0.012$ and $t = 2.472$, $P = 0.023$; Fig. 2a), with higher flowering density in the first year across treatments (Fig. 1). Warming also changed the density of anemone (Fig. 2b). The density was lower but not significantly so in warmed chambers compared to unwarmed controls in 2008, but the difference was significant in 2009 ($t = 6.646$, $P = 0.001$; Fig. 2b).

Larval damage on gentian reproduction

Damage from moth larvae on gentian flowers was dramatically enhanced by experimental warming ($t = 6.035$, $P < 0.001$ in 2008 and $t = 6.281$, $P < 0.001$ in 2009, Fig. 3a). Flowers were seriously damaged in all the warmed chambers while only one and two ambient chambers were found to have damaged flowers in 2008 and 2009, respectively. The damage percentages ranged between 70–80% in warmed OTCs whereas it was below 1% in control chambers of both 2008 and 2009 (Fig. 3a). Additionally more than 30% and 60% of the flowers successfully developed and fruited in the control chambers in 2008 and 2009, respectively (Fig. 3b). In contrast, fewer than 10% flowers bore fruit in the warmed OTCs. The percentage of initiated fruits was significantly lower in warmed chambers than in ambient controls in both years ($t = 10.513$, $P < 0.001$ and $t = 3.505$, $P = 0.004$; Fig. 3b).

DISCUSSION

Trophic disruptions have been recently suggested as a major cause for species loss under climate warming (e.g., Schwartz et al. 2006, Memmott et al. 2007, Tylianakis et al. 2008). Herein, we provide evidence consistent with this hypothesis, as our study showed that the gentian species experienced dramatic reductions in fruiting (and thus likely in seed production) due to a greatly increased

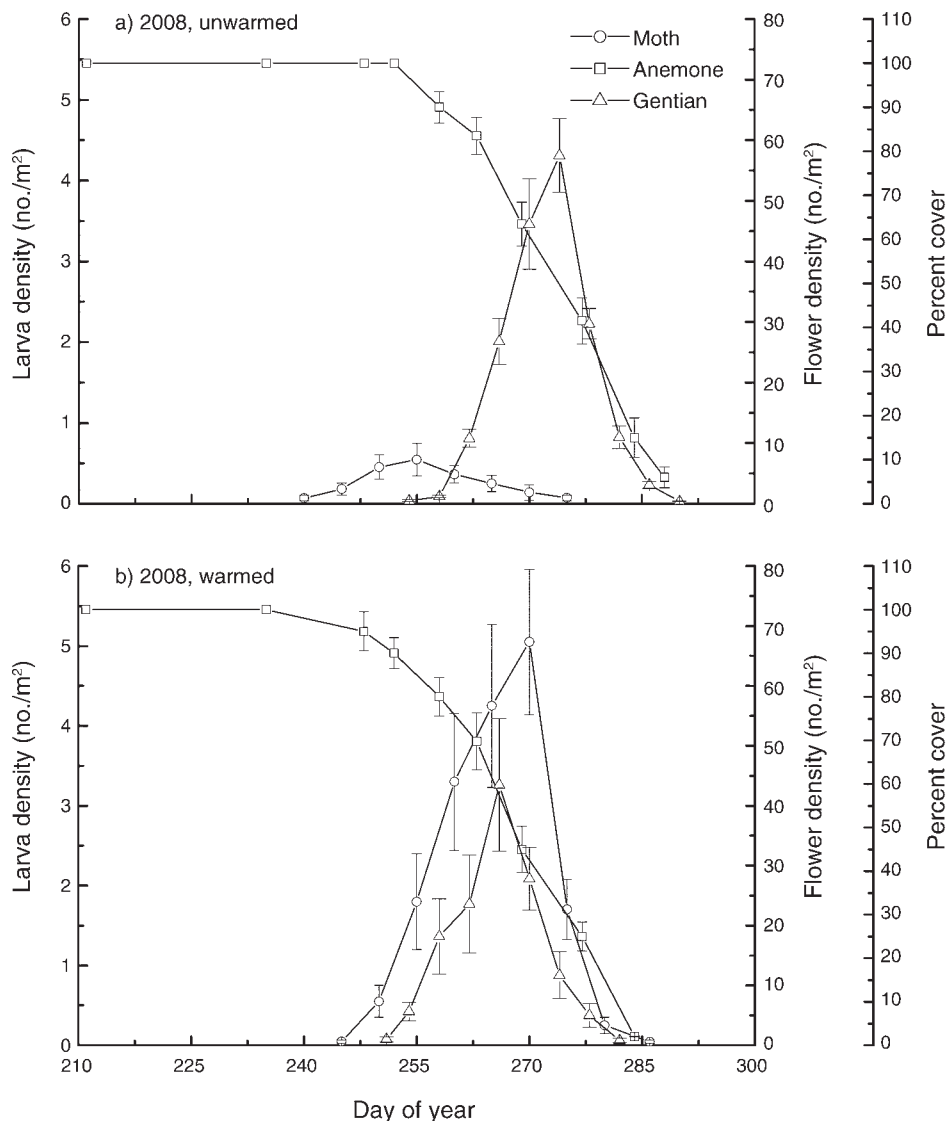


FIG. 1. The variation in larva density of the moth (*Melanchra pisi*), flower density of the gentian (*Gentiana formosa*), and percent cover of the anemone (*Anemone trullifolia* var. *linearis*) for unwarmed and warmed chambers in the years (a, b) 2008 and (c, d) 2009, where 1 January = day 1.

trophic relationship with an insect herbivore that normally very rarely attacks it. Experimental warming brought about simultaneous changes in both the phenologies and abundances of both species, making it possible for the moth and the gentian to create a major trophic connection.

As a late-flowering species in autumn, the gentian phenological advance is consistent with some terrestrial species (Visser and Holleman 2001, Visser et al. 2004, Memmott et al. 2007, Bertin 2008), but it differs from some other species that tend to delay flowering in warmed conditions (e.g., Sherry et al. 2007). This advance may be simply because the accumulated temperature above the minimum for flower development reached the threshold level for blooming earlier in the

warmed chambers. Another potential mechanism is that the timing of flowering is size dependent as plant height was progressively greater from 2008 to 2009, and plants were taller in the warmed OTCs than in the control chambers (Appendix D: Fig. D1a and b). It is possible that temperature and plant size might have collectively contributed to the observed changed flowering phenology in the gentian species.

The delay of larval emergence with warming is inconsistent with most previous studies on spring phenology of insects (e.g., Visser and Both 2005). Warming often advances both plant greening and bud burst and also emergences of insects (such as hatching of moth eggs; Visser and Holleman 2001). Cues such as temperature and photoperiod are often used to explain

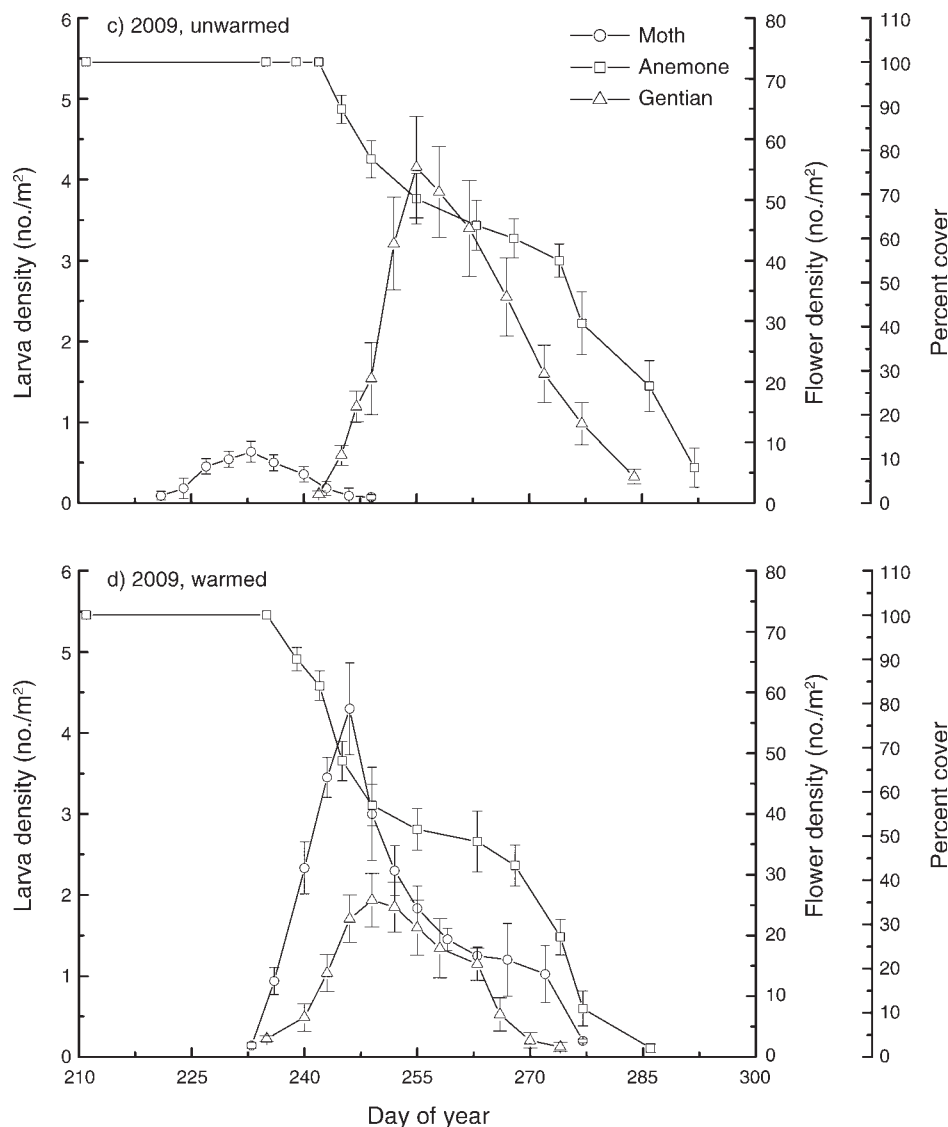


FIG. 1. Continued.

the onset of egg hatching and larvae emergence in different circumstances (e.g., Visser et al. 1998, 1999, Visser and Holleman 2001). In our case, photoperiod would not have differed between warmed and unwarmed chambers and hence cannot explain the difference in timing of larval emergence. In any case, although rare, our study is not the first to observe a delay of insect development with warming. Warming at cool temperatures delayed development of winter oak moths (*Operophtera brumata*; Visser et al. 1998, 1999). Our study site is cool, even in summer; hence, although the mechanism at work is unidentified, it is possible that delayed moth development with warming was following a similar mechanism in our study.

Experimental warming not only shifted the phenologies, but also significantly changed the densities for the

species. Larval abundance was much higher in the warmed chambers, consistent with general insect responses to temperature (Harrington et al. 2001, Bale et al. 2002). Larval outbreak was predictable provided that temperature increase facilitated egg hatching and larval development in the warmed chambers, particularly in the cold alpine meadow. Increased larvae density in the warmed chamber was not likely due to larva entering from outside the chambers as these were sunk into soil and high enough to prevent larva moving. Moth adults that were capable of flying over the chambers were not observed to visit the warmed chambers more frequently than the control chambers (Y. Liu and G. Li, *personal observation*); the physical barrier appeared to have similar effects on the insect behaviors for both types of OTCs.

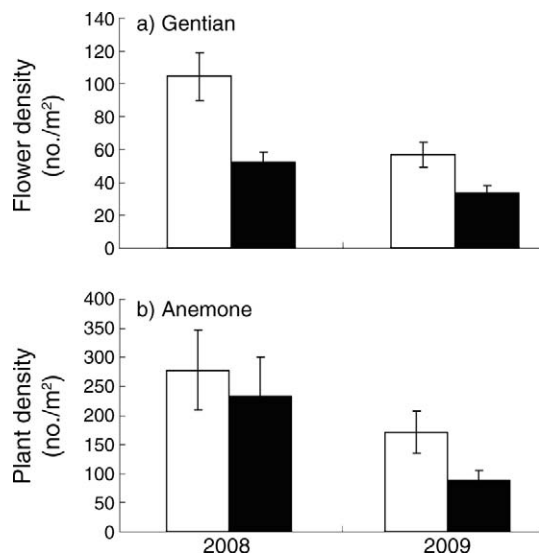


FIG. 2. (a) Flower density of the gentian species (*Gentiana formosa*) and (b) plant density of the anemone species (*Anemone trullifolia* var. *linearis*) for both the warmed chambers (black columns) and the unwarmed chambers (white columns) in the years 2008 and 2009. The error bars denote \pm SE. The sample size was 10 for each treatment.

As shown above, experimental warming significantly increased the abundance of the moth herbivore but significantly decreased the abundance and coverage (but not plant height) of the typical food species (the anemone; Fig. 2b; Appendix D: Fig. D1c and d) particularly during important periods of high larval density, and exposed the gentian flowers (including ovules) to the moth larvae by changing their phenologies. The damage percentage of the gentian flowers was not proportional to the peak density of the moth larvae between the warmed and unwarmed chambers. The flower damage was negligible ($<1\%$) in the unwarmed chambers (and only about 1% of that in the warmed OTCs), indicating that there was typically no substantive food relationship between the gentian and the moth larva. It is likely that shifts in both density and phenology of the species involved contributed to the radical change in trophic relationships observed from the ambient to warmed chambers. Previous studies have recorded diet shifts in warming experiments, but the shifting was often between two different normal host species (e.g., Bale et al. 2002, Barton and Schmitz 2009). In this study, however, we demonstrated that an extremely weak trophic relationship can become important under global warming.

One of the consequences of the altered trophic relationship was the significant loss of reproductive capacity in the gentian. We observed that the moth larvae directly fed on the flowers (and apparently there was only a small amount of damage caused by underground pests). Honeybees (*Apis cerana cerana*) occasionally visited the flowers of gentian in both

warmed and unwarmed chambers and they were more frequently observed in the warmed OTCs than in the ambient chambers in the late growing season, possibly because of relatively higher temperature in the warmed chambers. Therefore, the change in pollinator visitation rate could not account for the reduced seed production in the warmed chambers. Rodent activity was more apparent within warmed OTCs than in ambient controls, but the zokors mainly focused on the large rooted species without visible damage on the gentian. The loss of seed production (assuming a close relationship of seed production with fruit production) in a large proportion of the individuals might have partly contributed to the decrease in gentian dominance, as indicated by the lower density and coverage in the warmed OTCs than in the ambient chambers (Fig. 2b; Appendix D: Fig. D1a, b).

In conclusion, the results demonstrated that novel reformulations of trophic relationships can occur due to changes in phenology and abundances for both host and consumer species under climate warming. The consequence of the reformulation may change plant reproductive success at the species level and hence species composition at the community level, and in the long run could potentially contribute to species loss and change in ecosystem structure and function. Accordingly, the possibility of novel reformulations of trophic relationships should be seriously addressed in conservation biology and global change biology. The additional complexity contributed by such changes suggests that

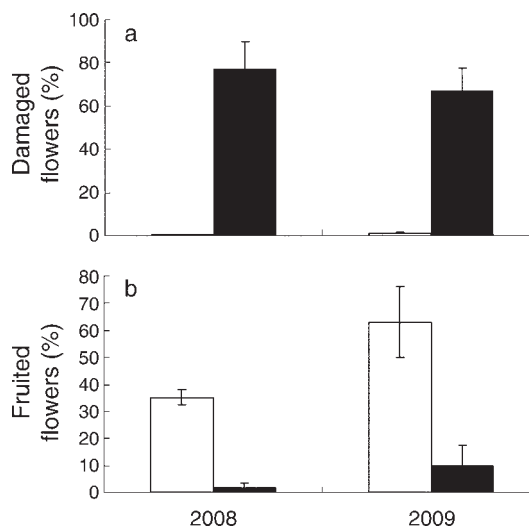


FIG. 3. The effect of damage by the moth larvae (*Melanchna pisi*) on reproductive capacity of the gentian species (*Gentiana formosa*) as indicated by (a) percentage of flowers damaged and (b) percentage of flowers that fruited for both the warmed chambers (black columns) and the unwarmed chambers (white columns) in the years 2008 and 2009. The damaged flower percentage is close to zero in the ambient chambers. The error bars denote \pm SE. The sample size was 10 for each treatment.

any predictions made about biodiversity distributions in a future warmed world are likely more uncertain than we might have previously thought.

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APPENDIX A

Schematic diagram showing trophic relationships among the moth larvae (*Melanchra pisi*) and the two plant species (*Gentiana formosa* and *Anemone trullifolia* var. *linearis*) (*Ecological Archives* E092-099-A1).

APPENDIX B

Descriptive statistics for the temperature differences at two levels of vertical profiles (*Ecological Archives* E092-099-A2).

APPENDIX C

Monthly means of soil moisture and daily means of relative humidity for measured periods (*Ecological Archives* E092-099-A3).

APPENDIX D

Plant height and percent cover of *Gentiana formosa* and *Anemone trullifolia* var. *linearis* (*Ecological Archives* E092-099-A4).